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NOTES ON THE GENUS *ZACOTUS* LE CONTE, 1869, AND ON THE CLASSIFICATION OF THE TRIBE BROSCINI (=BROSCIDAE SENSU JEANNEL, 1941. COLEOPTERA, CARABIDAE).

BY GEORGE E. BALL¹

1. INTRODUCTION

I became interested in the genus *Zacotus* several years ago. While examining a batch of undetermined Carabidae, I came across a fine series of specimens of this genus, the first I had ever seen, and was so taken by their bright color and graceful form that I determined to learn something about the species of *Zacotus*. These characteristics are hardly striking enough to capture the imagination of students of birds and butterflies, but they fairly dazzle those of us who deal with creatures as drab as most of the ground beetles are.

The first problem to be considered was the taxonomic validity of the names employed in *Zacotus*. Four names had been proposed, based on variation in color and sculpture, and later they were synonymized. Then Hatch (1953) divided the single species, *Zacotus matthewsii*, into two subspecies and two aberrations. Secondly, the taxonomic position of the genus needed to be investigated. Le Conte described *Zacotus* as a broscine. Horn (1881 : 169) erected the tribe Zacotini for this genus because it lacks a setigerous puncture in the scrobes of its mandibles, and so could not be a broscine. Sloane (1923 : 248) suggested that *Zacotus*, specimens of which he had not seen, may be a broscine, and in my opinion, he was right: *Zacotus* is a broscine. This decision created a third problem. If this genus belongs in the *Broscini*, then what are its relationships within the Tribe? Jeannel (1941) proposed a classification of the Family Broscidae (=Tribe Broscini) and divided the

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group into three subfamilies: Broscitae, Barypitae, and Creobitae. Some of the characters of *Zacotus* suggested that it should be placed in the Broscitae, others that it belonged in the Creobitae. It seemed impossible to place *Zacotus* in Jeannel's scheme, and this led me first to question the validity of his classification, and then to propose a slightly different one, based on a study of representatives of all of the broscine genera that could be obtained from the collections of the entomologically more important museums of North America. Britton (1949) presented an interpretation of the pattern of geographical distribution of the Broscini, and the assessment of this constitutes the final problem considered here.

II. ACKNOWLEDGMENTS

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Finally, I wish to thank Dr. B. Hocking for reading the manuscript, and for his many valuable suggestions arising therefrom, and Miss Ann Byrtus for typing the manuscript.

III. VARIATION IN THE GENUS *ZACOTUS*

The members of this rare genus are inhabitants of the forests of the Pacific Northwest (Hatch and Fender, 1944), ranging from at least northern California (Humboldt County) to southern Alaska (Dolomi, Prince of Wales Island), and eastward from Vancouver Island to the Bitter Root Mountains in extreme southwestern Montana. (see Fig. 1) Four specific names have been proposed in *Zacotus*: *matthewsii* Le Conte, 1869; *angustus* Casey, 1920; *subopacus* Hopping, 1925; and *fredericki* Nunenmacher, 1944. Hatch and Fender (1944) pointed out that these names were based on slight variations and that they applied to a single, variable species. The same conclusion was reached in this study,

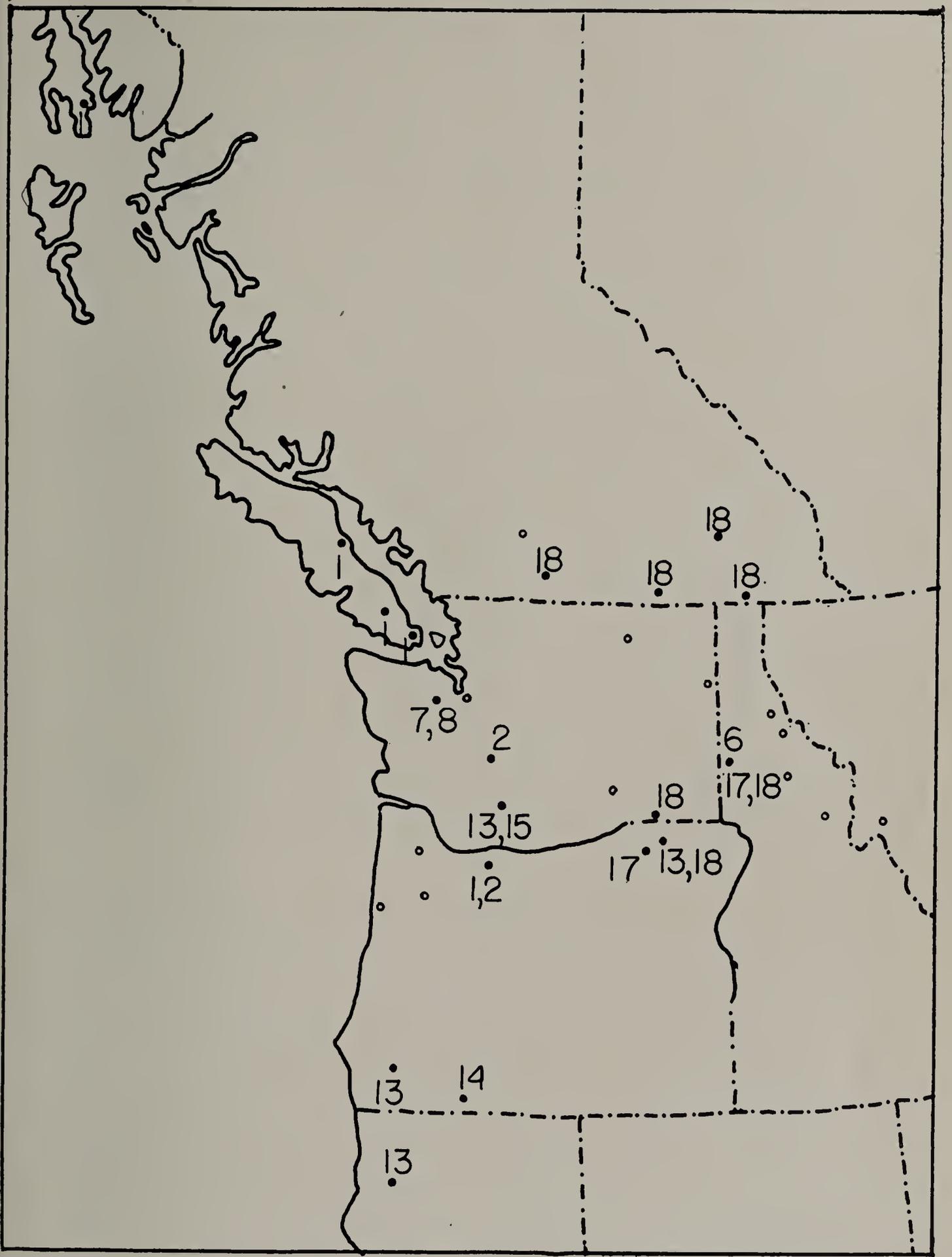


FIGURE 1. The distribution of *Zacotus matthewsii*. See text for explanation of numbers and symbols.

based on an examination of the external characters of fifty-six specimens. The male genitalia of ten specimens which represented three of the four named forms were found to be virtually identical. Representatives of typical *fredericki* were not seen. The oldest of the four names is *Z. matthewsii*, and this is, therefore, the name of this species.

Hatch (1953 : 186) presented in abbreviated form a classification of the populations of *matthewsii*, based on color of the dorsal integument. This classification is discussed below in terms of the characteristics of the specimens which I have seen.

Data on variation in color, luster and surface sculpture of the dorsal integument are presented in Table 1 and in Fig. 1. The localities in which specimens of *matthewsii* have been taken are indicated by circles in Fig. 1: empty circles represent localities which have been recorded by Hatch and Fender (1944); filled-in-circles represent localities from which I have seen specimens. The numbers near each filled circle indicate the characteristics of the specimens taken at the locality which is represented by the circle (see Table 1.). Color was assessed subjectively without reference to a standard chart. Variation in sculpture cannot be described very precisely but the impressions on the head and pronotum are usually deeper in western specimens than in eastern ones, so that the dorsal surface appears more coarsely sculptured in the former and more finely so in the latter. As an added complication, many specimens are intermediate between the extreme conditions. In the discussion which follows, the localities are grouped by their respective longitudes. Hatch and Fender (1944) characterized the specimens which they examined, and their observations are not repeated here.

TABLE 1.

NUMBERS ASSIGNED TO COMBINATIONS OF COLOR, LUSTER AND SCULPTURE OF THE INTEGUMENT OF THE DORSUM IN *Zacotus matthewsii*.

Color	Sculpture of Dorsal Integument		
	coarse	intermediate	fine
Metallic coppery	1	2	3
Dull coppery	4	5	6
Coppery-green	7	8	9
Green	10	11	12
Metallic violaceous	13	14	15
Dull violaceous	16	17	18

The Alaskan specimen was collected at Dolomi (55°08'N., 132° 03'W.).

Specimens with bright coppery integument in group 124.5-123.6°W. are from the following localities on Vancouver Island: Courtenay

(2 specimens), Findlayson (sic!) Flats (not plotted), Mt. Lehman (not plotted), Nanaimo, (2 specimens), Quamichan Lake (near Duncan), "Vancouver Island" (3 specimens) and Victoria. One of the "Vancouver Island" specimens is the type of *matthewsii* Le Conte (Le Conte Collection, Museum of Comparative Zoology, No. 5854, "Van"). Of two metallic violaceous specimens, one is the type of *angustus* Casey (Casey Collection, United States National Museum), Josephine County, Oregon, and the second was collected in "Humboldt County" California. The three empty circles in this group in Oregon represent Forest Grove, Salem, and Lincoln County (type locality of *fredericki* Nunenmacher).

The specimens included in group 123.5-122.6°W. were collected at Lake Cushman, Mason County, Washington (Nos. 7,8 on map). Of eight specimens, three have a coarsely sculptured integument, and five are classed as "intermediate."

Of three specimens in group 122.5-121.6°W. with bright coppery integument, two were collected on Mount Hood, Washington. One of these is as coarsely sculptured as is the type of *matthewsii*, while the other is somewhat less so. The third specimen with a coppery integument was collected on Mount Rainier, Washington (No. 2 on map), and its sculpture is classed as intermediate. The remaining specimen was taken five miles northeast of Pinehurst, Jackson County, Oregon, elevation 2000' (No. 14 on map). The empty circle in this group represents Seattle, Washington.

Group 121.5-120.6°W. includes specimens from three localities: Princeton, British Columbia, (2 specimens, including the type of *subopacus* Hopping, Canadian National Collection, Ottawa, No. 1380); Mount Adams, Yakima County, Washington (four specimens; the integument is metallic violaceous in one, dull in the other three); and Merritt, B. C. (represented by the empty circle).

The empty circles in group 120.5-119.6 represent Mount Bonaparte, Kanogan County, and Mt. Toppenish, Yakima County, Washington.

Group 119.5-118.6°W. includes specimen from four localities. Two specimens collected in a red cedar forest along Kettle Creek near Christina Lake, British Columbia, one from Walla Walla, Washington, (No. 18 on map) and three from Tollgate, Oregon, have finely sculptured, dull violaceous integuments. The integuments of two specimens from Meacham, Oregon (No. 17 on map), and one from Tollgate, Oregon, are metallic violaceous while the sculpturing is classed as intermediate. Another Tollgate specimen has a metallic violaceous, coarsely sculptured integument. The empty circle in northeastern Washington represents Newmar Lake, Spokane County.

The 117.5-116.6°W. group includes nine specimens collected in Latah County, Idaho. The integument of one specimen, taken at Moscow, Idaho, (Casey Coll.) is dull coppery. The sculpture of three of the remaining specimens is classed as intermediate, and as fine for five specimens. The British Columbia localities in this group are Creston (4 specimens) and Kaslo. The empty circles in Idaho represent Coeur D' Alene and St. Joe National Forests, Waha, and Pierce. The empty circle in Montana represents the Bitter Root Mountains.

The material available for study was insufficient to permit analysis of mensural characteristics. It is apparent to the unaided eye that Vancouver Island specimens average larger in size than specimens from the mainland. However, the following measurements of total length of females (length of head from the anterior margin of the clypeus to behind the eyes, plus the length of the pronotum along the mid-line plus the length of the elytra along the suture) show how slight the difference is: Vancouver Island, eight specimens, 15.2-18.0 mm; mean 16.7 mm; Mason County, Washington, five specimens, 14.4-17.0 mm; mean 15.9 mm; Latah County, Idaho, nine specimens, 15.3-17.0 mm; mean, 16.1 mm. The Vancouver Island specimens appear to be relatively wider also, but this is not borne out by the measurements.

These data seem to indicate that in general the integument of the reddish specimens is shining and coarsely sculptured, while that of the violaceous specimens is dull and less coarsely or finely sculptured. (The lack of perfect correlation indicates that all of the specimens are conspecific.) On the basis of these data it is possible to divide the species into eastern and western races. Four names are available. The type locality of *matthewsii* is Vancouver Island, and so this name applies to the western race. The name *fredericki* is based on a specimen collected in northwestern Oregon, with a bright green integument, and probably represents an extreme variant of the western race, or possibly an intergrading population. The dorsal integument is lustrous, as is that of the western race, but is relatively smooth, like that of the eastern race. The type specimen of *angustus* Casey exhibits the color of the eastern race and the sculpture and luster of the western one, and so this name seems to apply to an intergrade specimen, and not to either extreme. That leaves only *subopacus* Hopping to consider. The type locality, Princeton, B. C., is well within the range of the eastern race, and the characters of the type are those of the eastern race. Thus, this race may be called *Z. matthewsii subopacus*, and the western race, *Z. m. matthewsii*. This is essentially the arrangement presented by Hatch (1953: 186-187). However, he treated *fredericki* and *angustus*

as aberrations, whereas I do not think such action is necessary or desirable. Specimens referable to *fredericki* are either extremes of *m. matthewsii* or they possibly may be classed as intergrades, also.

The most interesting aspect of variation in *matthewsii* is the seeming discontinuity of color variation. The specimens of each population sample that I have examined and which has been reported on by Hatch and Fender (1944), excluding that from Latah County, Idaho, and the metallic green type of *fredericki* were either coppery, or violaceous. If this is correct then it is likely that the eastern and western races were separated from one another, possibly during the Pleistocene, and that the connection between them has been re-established relatively recently. If, on the other hand, variation is continuous (i.e., a gradual shift in percentage of reddish to violaceous individuals from west to east) so that a sharp line cannot be drawn between the eastern and western populations, then it would seem unlikely that there had been a major break in the range of the species. If the latter proves to be the case and variation turns out to be clinal then it would be profitable to abandon subspecific names in *matthewsii*. Large series of specimens are needed from many localities, especially in the central Cascades, before we begin to understand the distribution of color in this species.

IV. RELATIONSHIPS OF *Zacotus*

Horn (1881 : 169) believed that the absence of setae from the scrobes of the mandibles was characteristic of *Zacotus*, and mainly for this reason, he removed this genus from the Broscini. However, of fifty-six specimens examined by me, seven lack the setae from both mandibles, twelve have a seta in the scrobe of one mandible, but not in the other, while thirty-seven have setae in the scrobes of both mandibles. Further, the New Zealand broscines *Mecodema*, *Metaglymma* and *Brullea* lack the mandibular setae, so that this particular feature is not characteristic of all broscine genera. The data in Table 2 show that the combination of morphological features which characterize the Broscini are possessed by *Zacotus*. Therefore, there seems to be no valid reason for excluding this genus from the Broscini.

Bradley (1930) included *Zacotus* in the Broscini, but his key to the genera is not altogether satisfactory because it depends upon the presence or absence of mandibular setae to separate this genus from the other North American broscine, *Miscodera*. However, the following key should give satisfactory results:

Dorsal surface of head with several longitudinal grooves; ventral surface with two deep, transverse grooves on either side of gula; mentum with ventral surface almost plane, not deeply impressed on each side of tooth; elytra with 5-12 punctures in the lateral umbilical series.....*Zacotus* Le Conte.

Dorsal and ventral surfaces of head smooth; mentum with a deep circular impression either side and basad of tooth; elytra with 2-4 punctures in the lateral umbilical series.....*Miscodera* Eschscholtz.

TABLE 2
CHARACTERISTICS OF THE BROSCINI AND OF *Zacotus*

Characteristics	Broschini	<i>Zacotus</i>
Shape of body	pedunculate	pedunculate
No. glabrous ant. segs.	1-4	4
Seta in mandibular scrobe	present or absent	present or absent
Front tibiae	anisochaetous	anisochaetous
Front coxal cavities	uniperforate	uniperforate
Middle coxal cavities	closed by sterna	closed by sterna
Elytral plica	present, not interrupting inflexed margin toward apex	present, not interrupting inflexed margin toward apex
Male genitalia, lateral lobes	setiferous	setiferous

V. CLASSIFICATION OF THE BROSCINI

THE SUBTRIBES.—Jeannel (1941: 287-288) presented an abbreviated classification of this family² (tribe) and based his subfamilial (subtribal) categories on details of the basal orifice of the median lobe, and setosity of the left lateral lobe. (see Table 3.) In two footnotes on page 289 in the above reference he states that "the species of the

TABLE 3.
JEANNEL'S CLASSIFICATION OF THE FAMILY BROSCIDAE

Characteristics	Subfamilies		
	Barypitae	Creobitae	Broschitae
Median lobe, basal orifice	closed dorsally	open dorsally, opening long	open dorsally, opening short
Left lateral lobe	not setiferous	not setiferous	setiferous
Included Genera	<i>Barypus</i> <i>Cardiophthalmus</i> <i>Mecodema</i> ³ <i>Brullea</i> ³ "numerous others"	<i>Creobius</i> <i>Promecoderus</i> <i>Miscodera</i> ³ <i>Broscodes</i> ⁴ <i>Broskosoma</i> ³	<i>Broschus</i> ³ <i>Craspedonotus</i> ³ <i>Chaetobroschus</i> ³ <i>Axonya</i> ³

²Although I admire Jeannel's classification of the Carabidae (*sensu latiore*), I am not prepared to accept either his elevation of the tribes to family status or his reasons for doing so. Britton (1949: 533) has already discussed these points, and I agree with his conclusions.

³Genera having sclerites *x* and *y* in the median lobe.

⁴I have not seen a representative of this genus.

gondwanian lineage, especially the Creboitae, are generally of a metallic color, coppery red or green" and that "the umbilical series is again more specialized in the Creobitae, reduced to a very small number of large pits" (my translation). Thus he indicates that these features have appreciable classificatory value. However, *Zacotus*, *Miscodera* and *Broscosoma* cannot be placed very satisfactorily in this scheme, for the following reasons.

The extent of the dorsal emargination of the basal orifice does not seem to be a particularly reliable taxonomic character. The numerical value for total length of median lobe divided by the length of the dorsal emargination varies from 0 in Jeannel's Barypitaie to 0.76 in the genus *Creobius*. Approximate values for a single representative of each of the following species are: *Zacotus matthewsii*, 0.17; *Axonya championi*, 0.20; *Broscus cephalotes*, 0.25; *Craspedonotus tibialis*, 0.25; *Broscosoma baldense*, 0.30; *Parroa noctis*, 0.30; *Cerotalis* sp. 0.30; *Miscodera arctica*, 0.43; and *Promecoderus howitti*, 0.50. There are no sharp breaks in this series, but if the classification is based on this character, there is no doubt that *Zacotus* goes with *Broscus*. Also, as in the Broscitae, the left lateral lobe of *Zacotus* bears several setae apically (Fig. 4 C). The punctures of the umbilical series in *Zacotus* range in number from five to twelve per elytron, but these vary to such an extent through the Broscini that their taxonomic value must be slight. On the other hand, the metallic color of its integument suggests that *Zacotus* belongs with the Creobitae. A somewhat similar picture emerges when the characteristics of *Miscodera* and *Broscosoma* are considered. The dorsal emargination of the basal orifice is not much greater in *Broscosoma* than it is in *Broscus*, and *Miscodera* falls about midway between *Broscus* and *Creobius* with respect to this character. Thus the placing of *Broscosoma* and *Miscodera* on the basis of this character is equivocal, but they go with Creobitae in color, in having a reduced number of umbilical punctures on the elytra, and in lacking setae on the left lateral lobe. These facts seemed to indicate that the morphological foundation of Jeannel's classification was weak. Further, I found that the genitalia of *Zacotus*, *Miscodera* and *Broscosoma* agree with those of *Broscus* in what seems to be an important structural detail, which is described below. Because of these considerations, the structure of the male genitalia was reinvestigated. Three different types were found, and were used as the morphological basis for three subtribal groups. See Table 4 for a summary of the characteristics of the genitalia, and a list of the genera which have each type; see also Figs. 2-17.

TABLE 4.
SUGGESTED REARRANGEMENT OF THE BROSCINE GENERA⁵

Characteristics	Subtribes		
	Barypina	Creobiina	Broscina
Median lobe, basal orifice	closed dorsally	open dorsally	open or closed dorsally
Median lobe, dorsal surface	completely sclerotized	completely membranous	partly sclerotized to completely membranous
Basal keel	present	absent	absent
Sclerites x and y	absent	absent	present
Included genera	<i>Barypus</i> (s. lat.) S.A.	<i>Creobius</i> , S.A. <i>Cascellius</i> , S.A. <i>Promecoderus</i> , Aust. <i>Parroa</i> , Aust. <i>Gnathoxys</i> , Aust. <i>Cerotalis</i> , Aust.	<i>Axonya</i> , India <i>Craspedonotus</i> , Asia <i>Chaetobroscus</i> , Asia <i>Broscus</i> , Eurasia. <i>Zacotus</i> , Nearctic <i>Miscodera</i> , Holarctic <i>Broscosoma</i> , Eurasia <i>Diglymma</i> , N. Z. <i>Oregus</i> , N. Z. <i>Metaglymma</i> , N. Z. <i>Mecodema</i> , N. Z. <i>Brullea</i> , N. Z. <i>Percosoma</i> , Aust. <i>Eurylychnus</i> , Aust.

⁵Genera not seen: *Broscodes*, Persia; *Chlynus*, Aust.; *Percolestus*, Aust.; *Brithy-sternum*, Aust.; *Acallistus*, Aust.

Five points concerning the structure of the male genitalia are worthy of mention. First, the extent of the dorsal emargination of the basal orifice of the median lobe varies too much intergenerically to be useful as a major taxonomic character. Its depth varies from 0.0 to 0.43 of the length of the median lobe within the Broscina, as defined here. Second, the presence or absence of setae on the left lateral lobe is not of great importance in this group. Third, the internal sac of the Barypina is everted from the left side, whereas in the other two groups, the sac is everted from the dorsal side. Fourth, the genera included in the Creobiina are a diverse lot, and further study may show that the group as constituted here should be divided into several subtribes. Fifth, the sclerites associated with the internal sac of the Broscina have not been described previously. (see Fig. 3.) Three sclerotized regions are associated with the internal sac. The apical plate lies nearest the apex when the sac is in the inverted position, and is inside the walls of the sac. This plate is lightly sclerotized, complicated in shape, and in most of the illustrations, it is shown only in outline. The apical

plate is attached by membrane along its ventral side to the internal sac and its dorsal surface is partly covered by, but not attached to, a more or less cup shaped sclerotized area. This latter sclerotization is on the outer surface of the internal sac. For descriptive purposes, I have designated it as "sclerite y." Based is a curved, elongate trough-like structure, "sclerite x," which is on the basal dorsal surface of the internal sac. The ventral surface of sclerite x is covered by a membrane which appears to be a continuation of the internal sac, and the entire structure probably surrounds that portion of the ejaculatory duct which extends into the median lobe. When the internal sac is everted, and this can be accomplished with difficulty, sclerite x moves distad with the internal sac, but it remains within the median lobe. The origin and function of this peculiar structure is unknown to me.

I believe that the forms which have sclerites x and y should be placed in a single group. By contrast, if Jeannel's scheme is accepted then one of two postulates regarding the phylogeny of the Broscini must be accepted also: either that the ancestral stock of each group possessed these sclerites, and that they were lost in each of the three phyletic lines; or that the ancestral stock did not possess this feature, and that it was evolved independently in each line. I doubt that the ancestral stock of the Broscini possessed these sclerites, that such a complicated structure would be developed independently three times, and that once evolved it would be lost in each line. Therefore, I reject both of the above postulates.

In spite of the slight modifications that have been made in Jeannel's scheme it is apparent that he made a major contribution to the classification of the Broscini by his study of the male genitalia. Equally important was his discovery that *Cnemacanthus* (*sens. lat.*) was not even related to the broscines, but that this genus belonged in the Conchifera (see Figs. 17 a and b, illustrating the glabrous, conchiferous lateral lobes of *Cnemacanthus araucanus*).

In the course of this study, I have examined a number of other characters, such as the number of glabrous segments of the antennae; shape of the palpi; setae of the ligula, head, pronotum, and abdomen; color; number of punctures in the umbilical series of the elytra; specialization of the fore and middle tarsi of the males; and the scutellar (morphological first) and second striae of the elytra. All of these features were found to exhibit both inter and intrageneric variation, but the pattern of variation did not show any significant trends or coincide with the pattern of variation of the genitalia. For example, males of *Promecoderus* have spongy pubescence on the first four tar-

someres of the front and middle tarsi, but the tarsi of males of the closely related *Anheterus gracilis* are without spongy pubescence. (As a matter of fact, these two groups are very probably congeneric.) The front and middle tarsi of *Creobius*, *Cascellius*, and several genera of the subtribe Broscina also have spongy pubescence ventrally. Thus, if this character were relied on, several different forms would be grouped together, while otherwise similar forms would be placed in different groups.

Specimens of *Broscus* have a single puncture bearing a single seta over each eye, while individuals of the seemingly closely related *Chaetobroscus* and the seemingly unrelated *Creobius* have three or four supra-orbital punctures over each eye. Glabrous fourth antennal segments are characteristic of *Broscus*, whereas the apical halves of the fourth antennal segments are hairy in the closely related *Craspedonotus*. Mandibular setae are lacking in three closely related genera of the Broscina, but these setae are present in all of the remaining broscine genera seen in this study. The posterior pair of pronotal setae are lacking in *Miscodera arctica*, but are present in *M. insignis*, as well as in all of the other species that I have examined. The base of the second elytral stria is present in some species of *Broscus*, whereas it is absent in other species. The female retractile plates do not offer characters. Thus the division into subtribes is based only on the structure of the median lobe and internal sac of the genitalia.

RELATIONSHIPS OF THE SUBTRIBES.—The three groups recognized here seem to be structurally about equidistant from one another, and it appears impossible to derive any one group from any other. This suggests that the Broscini has had a long history, and that a large fragment of it is lost to us.

CLASSIFICATION OF THE BROSCINA.—The genera included here may be arrayed as follows: a. those with a keeled ligula, dorsal surface of the median lobe partly sclerotized, basal orifice closed dorsally, and with an elongate sclerite x, which lacks lateral upturned projections—the New Zealand genera (see Figs. 11 and 12); b. those with an unkeeled ligula, dorsal surface of the median lobe partly or not sclerotized, basal orifice open dorsally, and with an elongate sclerite x which has lateral upturned projections—the Oriental-Palaeartic-Nearctic genera, excluding *Axonya championi* (see Figs. 2-9) c. the genus *Axonya*, with an unkeeled ligula, dorsal surface of the median lobe unsclerotized, basal orifice open dorsally, and with a short sclerite x which lacks lateral projections. (see Fig. 10.) I suggest that each of these groups is

monophyletic, and that of the three, *Axonya* is the most primitive. I cannot place the Australian *Eurylychnus* and *Percosoma* in this scheme because I did not study them with sufficient care and have not had the opportunity to re-examine them.

Of the New Zealand genera, *Diglymma* and *Oregus* seem to be more primitive than the other three as is indicated by the characters in the first couplet of Britton's key (1949 : 538). Further the scutellar stria is preserved in *Diglymma* and *Oregus*, and their elytra are flat basally; in *Metaglymma*, *Mecodema*, and *Brullea*, on the other hand, the scutellar stria is absent, and the elytra are ridged toward the base.

The genera of the Old and New World, excluding *Axonya*, are all so very similar structurally that they could easily be included in a single genus. However, the species included in each of the present genera are more similar to their respective congeners than they are to the species of any other genus. Thus the genera seem to be natural, and it is only a matter of changing their taxonomic rank. I am not prepared to implement this suggestion at present because I have not seen representatives of all of the Broscini. The six Holarctic genera with which I am familiar seem to form two minor phyletic arrays: one including *Broscus*, *Chaetobroscus*, and *Craspedonotus*—they have about the same pronotal shape, and only the basal tarsomeres of the front tarsi bear spongy pubescence or none at all; a second including *Zacotus*, *Miscodera*, and *Broscosoma*, the males of which have spongy pubescence on the basal tarsomeres of the front and middle tarsi.

NOTES ON THE CREOBIINA.—I have studied critically only a few specimens of this group, including *Cascellius gravesi*, *Creobius eydouxi*, *Promecoderus howitti*, and a species of *Parroa*. The species representing *Cascellius*, and *Promecoderus* have four setae on the ligula, while this structure in *Parroa* bears only two setae, apically. In the males of *Creobius*, *Cascellius*, and *Promecoderus* (excluding *A. gracilis*) the basal four tarsomeres of the front and middle tarsi bear spongy pubescence, while in *Parroa* they are without the pubescence. The male genitalia of *Creobius* and *Cascellius* (Fig. 13) are quite similar and the internal sac in each genus is expanded ventrally to form a pouch, the latter curving part way around the rest of the sac. The internal sac in *Promecoderus* is folded longitudinally, and is armed internally with small spines (Fig. 14 A). The internal sac of *Parroa* bears a very large spine attached to a broad plate on the left side (Fig. 15). The genitalia and fascies of *Cascellius* and *Creobius* are so similar that the two may be regarded as congeneric, but the difference in the genitalia

of these and the other two genera is of greater magnitude than that which occurs intergenerically in the Broscina.

VI. THE GEOGRAPHICAL DISTRIBUTION OF THE BROSCINI

Britton (1949), in his outstanding work on the Broscini of New Zealand, suggested that this tribe was of Cretaceous palaeantarctic origin because of the relatively greater diversity of the Broscini on the southern land masses, and because of its restriction to the temperate parts thereof. Further, he states that the Broscini probably reached South America by way of a southern land connection, and spread in early Tertiary time from there through northern Africa to the Palaearctic, by way of a land connection from northern South America to the Mediterranean region. He does not accept invasion of the northern hemisphere by way of Asia because "the Palaeantarctic continent was separated from Asia from the end of the Jurassic until the late Tertiary so that the Broscini could not have reached Asia directly from Australia sufficiently early to allow for the considerable diversification of the Palaearctic genera and species." I question parts of this, first, because it seems to be an unnecessarily complicated hypothesis to explain the distribution pattern of the extant Broscini, and second, because the land bridges mentioned are not supported by any geological evidence known to me. A different point of view, based on my understanding of the taxonomy and distribution pattern of this tribe follows.

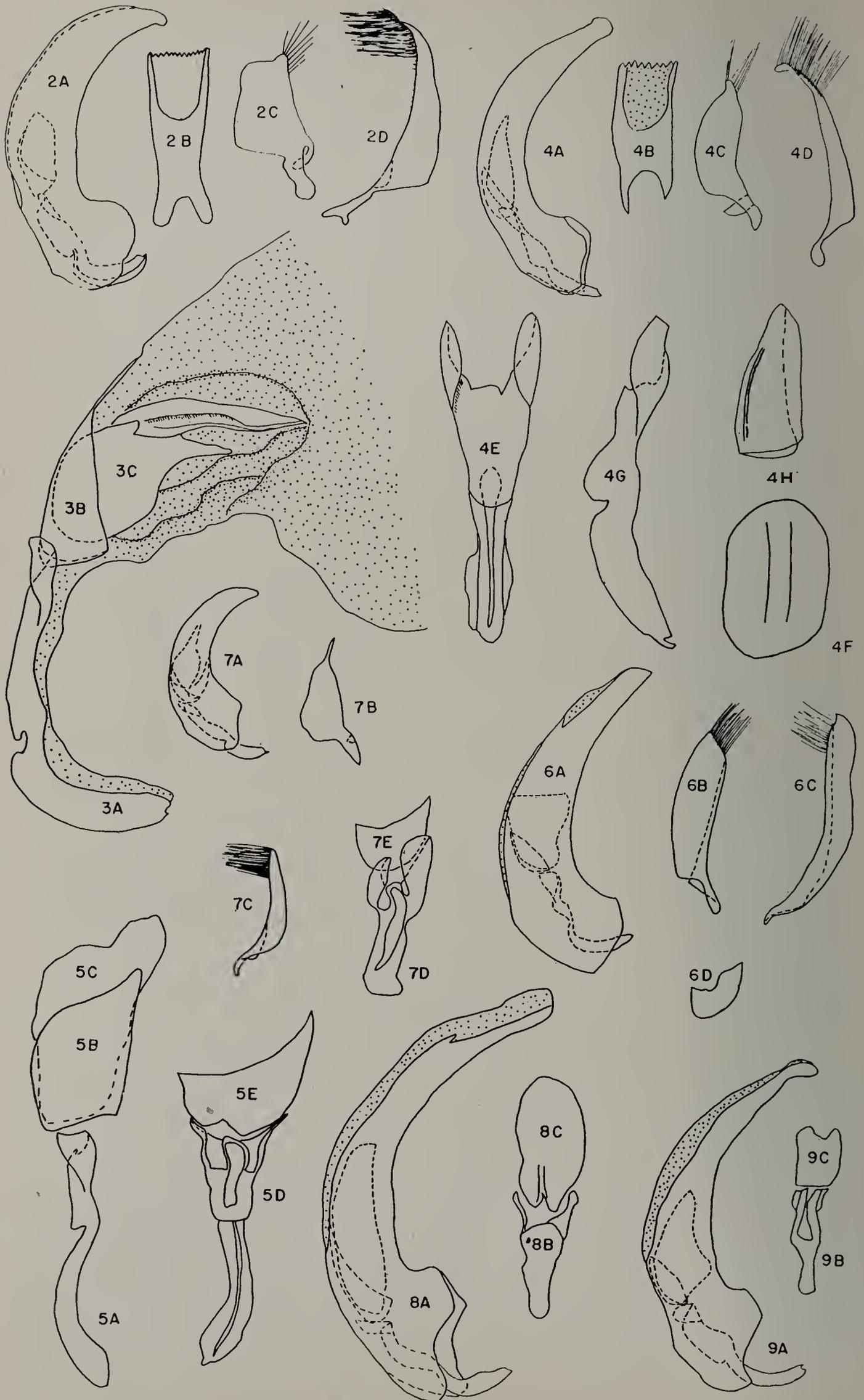
Of the three subtribes, the Barypina are restricted to southern South America, the Creobiina as defined here are found in southern South America, and in western Australia, but nowhere else, and the Broscina occur in New Zealand, Australia, and on the northern land masses (see Fig. 18). It is likely that the ancestral stocks of the Barypina and Creobiina arose in the southern hemisphere, and I consider it possible that they reached South America by way of a southern route. Possibly the ancestral stock of the extant Barypina arose in southern South America. There is no evidence against this point of view.

Whether invasion of South America took place by dispersal from island to island or by way of a direct land connection across the southern polar region, it is impossible to say. However, geological data do not support a direct land connection between South America, Antarctica, New Zealand and Australia.

The distributional data do not support the hypothesis that the Broscina reached the Palaearctic by way of South America. This subtribe, the only one of the three known to have representatives in the northern hemisphere is not represented in South America, and the

center of abundance of the group seems to be in the eastern Palaearctic. The distribution pattern suggests to me that the ancestral stock of the Broscina arose in the southeastern Palaearctic or in Australia and dispersed from either of these centers possibly by way of what is now the Indo-Australian Archipelago. Open stretches of sea may have been crossed by flight, or by other means. If the dispersing stock was adapted to temperate conditions, then it probably spread by flight from mountain top to mountain top across the tropical areas of the Old World to the Himalayas proper and thence farther northward, eastward and westward. However, dispersal did not have to take place by these means. Possibly one stock of Broscina was adapted to tropical conditions, and dispersed across the tropical areas of the Old World; from this stock evolved the extant temperate adapted broscine genera of the Holarctic. Probably, one stock of Broscina got to New Zealand from Australia, over the sea. Another possibility remains to be considered; one portion of the ancestral stock of the extant Broscina of the northern hemisphere may have reached South America by a southern route, dispersed northward, reached the northern hemisphere by way of North America, spread to the Palaearctic from the west, and ultimately died out in South America and in most of North America. This is possible but it is not supported by the distribution of the extant genera.

By way of summary, I consider it likely that the Broscini arose in the southern hemisphere and became widespread there, probably in Mesozoic time. South America may have been invaded twice: once by the stock that gave rise to the Barypina, and once by the Creobiina. The Palaearctic was invaded from the west, the Canary Islands from the western Palaearctic, and North America, possibly by way of the Bering Strait land bridge. New Zealand probably received its single original broscine stock from Australia. This hypothesis has no more positive evidence to support it than has Britton's, but I think that the circumstantial evidence is better. However, I wish to emphasize that the geographical distribution of the extant Broscini can tell us nothing about earlier land connections or former locations of continents, or whether or not the continents have changed positions, but rather if we knew more about such topics then we would know more about the probable routes and times of dispersal of the Broscini. Darlington (1952: 215-216) made a similar point with reference to the invertebrate fauna of South America, and I feel that it is applicable to a discussion of the distribution of this tribe.



(Figures 2-9, p. 48)

FIGURE 2. Male genitalia of *Broscus cephalotes*, 33x. A. Median lobe, left lateral aspect B. Base of median lobe, dorsal aspect C. Left lateral lobe D. Right lateral lobe.

FIGURE 3. Lateral aspect of sclerites x and y, with the membranous portion of the internal sac slit open to expose the apical plate of *Broscus cephalotes*, Turkestan (Ball Collection), 66x. A. Sclerite x B. Sclerite y C. Apical plate.

FIGURE 4. Males genitalia of *Zacotus matthewsii* Le Conte, Washington Territory, (Academy of Natural Sciences of Philadelphia). A. Median lobe, left lateral aspect, 33x B. Base of median lobe, dorsal aspect C. Left lateral lobe, 33x D. Right lateral lobe, 33x E. Sclerite x, dorsal aspect, 66x F. Sclerite y, dorsal aspect, 66x G. Sclerite x, left lateral aspect, 66x H. Sclerite y, left lateral aspect, 66x.

Figure 5. Sclerites of internal sac of *Chaetobroscus anomalus* Chaudoir, Jaloor, Kulu; (California Academy of Sciences). 66x. A. Sclerite x, left lateral aspect B. Sclerite y, left lateral aspect C. Apical plate, left lateral aspect D. Sclerite x, dorsal aspect E. Sclerite y, dorsal aspect.

FIGURE 6. Male genitalia of *Craspedonotus margellanicus* Kratz, Turkestan (Ball Collection), 33x. A Median lobe, left lateral aspect B. Left lateral lobe C. Right lateral lobe D. Sclerite y of internal sac, dorsal aspect.

FIGURE 7. Male genitalia of *Miscodera arctica* Paykull, St. Geo. Bay, Nfld., (University of Michigan, Museum of Zoology). A. Median lobe, left lateral aspect, 33x B. Left lateral lobe, 33x C. Right lateral lobe, 33x D. Sclerite x, dorsal aspect, 66x E. Sclerite y, dorsal aspect, 66x.

FIGURE 8. Male genitalia of *Miscodera insignis* Mannerheim, Ranier Nat. Pk. Wash., (California Academy of Sciences). 66x. A. Median lobe, left lateral aspect B. Sclerite x, dorsal aspect C. Sclerite y, dorsal aspect.

FIGURE 9. Male genitalia of *Broscosoma baldense* Rosch., Monte Baldo, Switzerland, (California Academy of Sciences). 66x A. Median lobe, left lateral aspect B. Sclerite x, dorsal aspect C. Sclerite y, dorsal aspect.

(Figures 10-17, p. 50)

FIGURE 10. Male genitalia of *Axonya championi* Andrews, India, (California Academy Of Sciences). 150x A. Median lobe, left lateral aspect B. Left lateral lobe C. Sclerite x., dorsal aspect D. Sclerite y, dorsal aspect E. Apical plate, dorsal aspect.

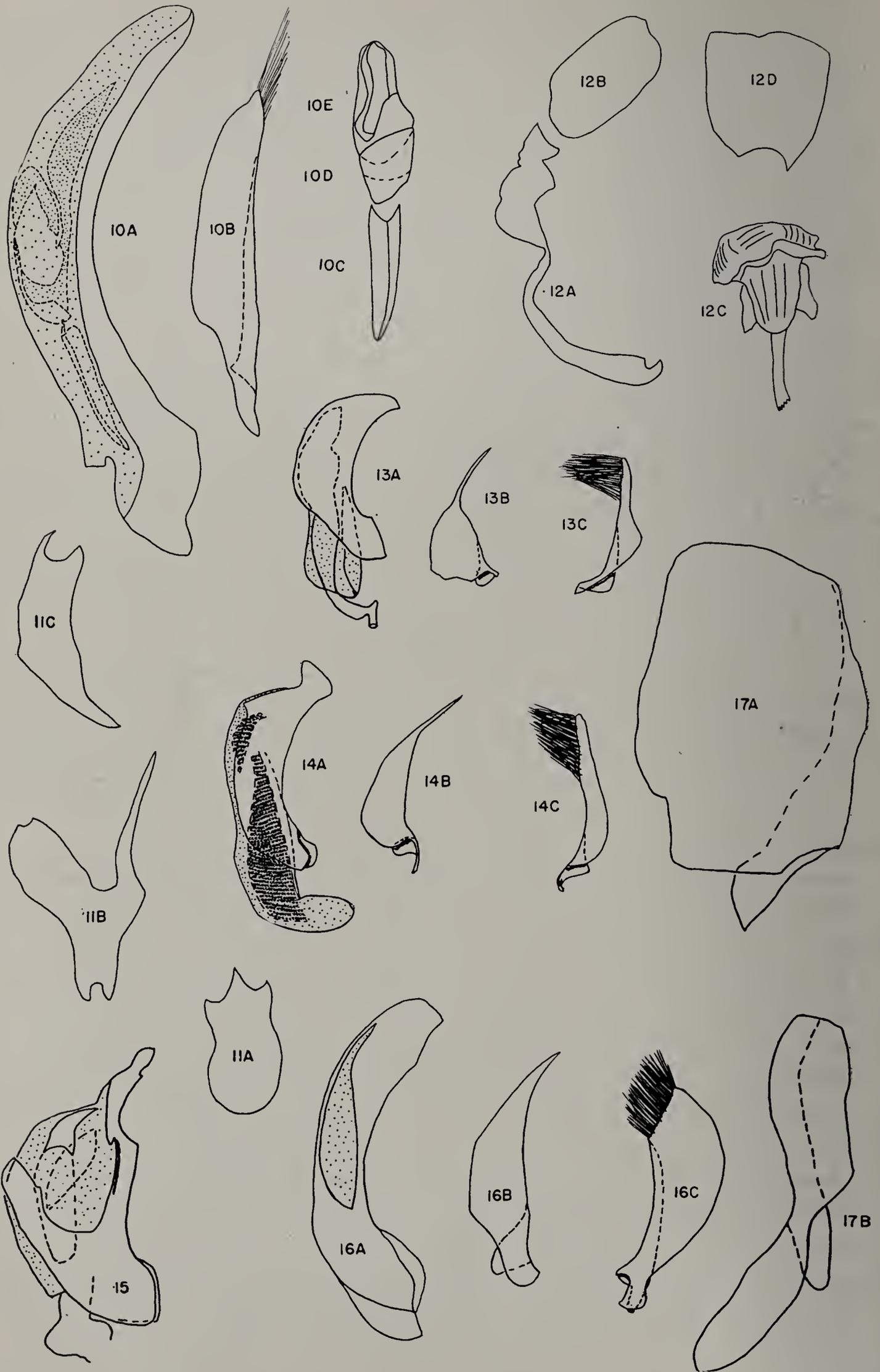
FIGURE 11. Sclerites of internal sac of *Diglymma ovipenne* Sharp, Cass, New Zealand (California Academy of Sciences). 66x A. Sclerite x, dorsal aspect B. Sclerite y, dorsal aspect C. Sclerite x, left lateral aspect.

FIGURE 12. Sclerites of internal sac of *Brullea antarctica* Castelnau, N. Karamea, New Zealand, (California Academy of Sciences). 66x A. Sclerite x, left lateral aspect B. Sclerite y, left lateral aspect C. Sclerite x, apical portion, dorsal aspect D. Sclerite y, dorsal aspect.

FIGURE 13. Male genitalia of *Cascellius gravesi* Curtis, Punta Arenas, Chile, (Museum of Comparative Zoology). 33x. A. Median lobe, left lateral aspect B. Left lateral lobe C. Right lateral lobe.

FIGURE 14. Male genitalia of *Promecoderus howitti* Castelnau, Dunkeld, Victoria, Australia, (Academy of Natural Sciences of Philadelphia). 33x A. Median lobe, left lateral aspect B. Left lateral lobe C. Right lateral lobe.

(Continued on p. 51)



(Figures 10-17, p. 50)

(Continued from p. 49)

FIGURE 15. Median lobe, left lateral aspect, of *Parroa* species? Australia, (American Museum of Natural History). 33x.

FIGURE 16. Male genitalia of *Barypus* species? , Neuquen, St. Martin de los Andes, Argentina. (Ball Collection). 33x A. Median lobe, left lateral aspect B. Left lateral lobe C. Right lateral lobe.

FIGURE 17. Lateral lobes of *Cnemacanthus araucanus* Germain, 22 mi. N. of Talca, Chile, (California Academy of Sciences). 66x A. Left lateral lobe B. Right lateral lobe.

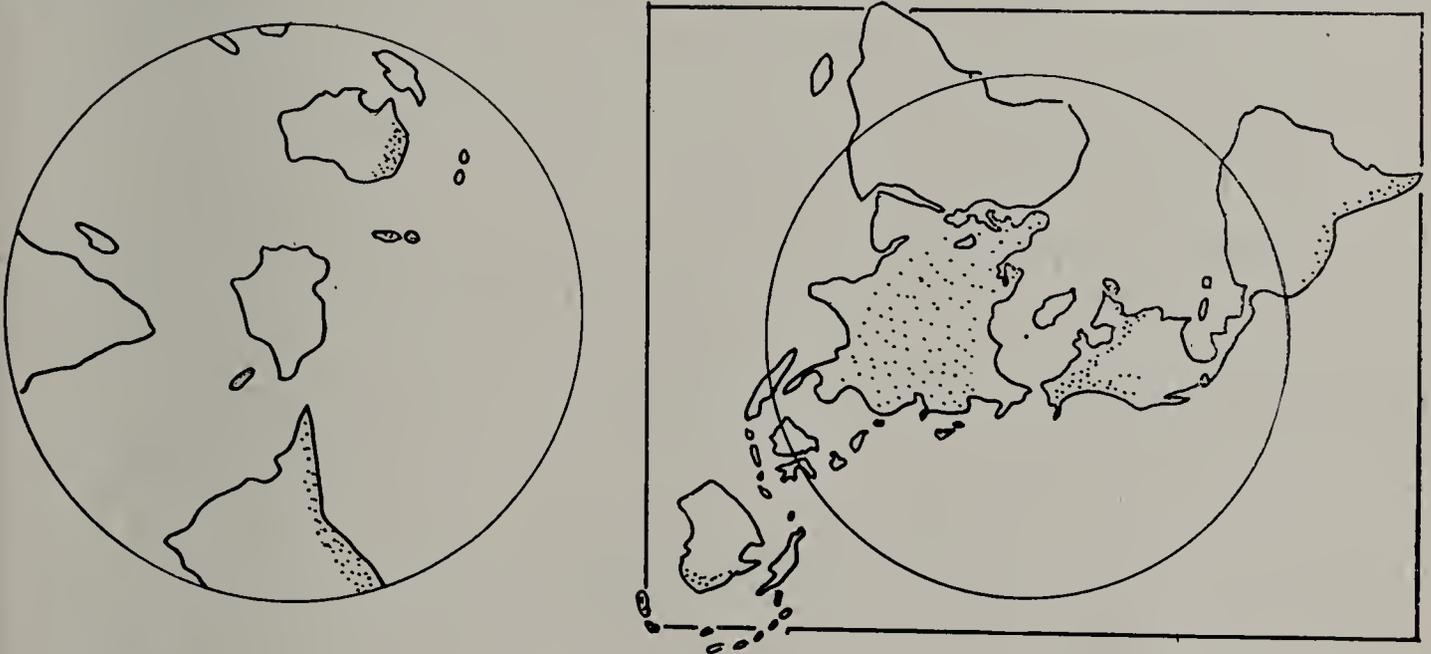


FIGURE 18. The distribution of the Tribe Broscini (Broscines are known to occur in the stippled area). At left, north polar projection; at right, south polar projection.

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